RELATIONSHIPS BETWEEN ECOSYSTEM METABOLISM, BENTHIC MACROINVERTEBRATE DENSITIES, AND ENVIRONMENTAL VARIABLES IN A SUB-ARCTIC ALASKAN RIVER

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A

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Abstract

The aim of this study was to investigate the environmental drivers of river ecosystem metabolism and macroinvertebrate density in a sub-arctic river. Ecosystem metabolism is the combination of gross primary production and ecosystem respiration within a river. Aquatic macroinvertebrates link primary producers at the base of the food web with secondary consumers. The extent to which photosynthetically active radiation, discharge, and nutrients influence metabolism rates and how primary production and river discharge rates influence benthic macroinvertebrate densities in sub-arctic rivers is not clear. These processes ultimately help regulate prey resources available for upper level consumers such as juvenile salmon. I employed Random Forests model analyses to identify important predictor variables for primary production and respiration rates (estimated using the single-station diel oxygen method) at four sites in the Chena River, sub-arctic Alaska, throughout the summers of 2008 and 2009. I calculated Spearman correlations between nutrient levels and metabolism rates. I used Random Forests models to identify the variables important for predicting benthic macroinvertebrate density and biomass at the study sites. The models indicated that discharge and length of time between high water events were the most important variables measured for predicting metabolism rates. Discharge was identified as the most important variable for predicting benthic macroinvertebrate density and biomass. Phosphorus concentration was low (at times below the detection limit), while nitrogen concentration was more variable; the ratio of nitrogen to phosphorus was above the threshold for phosphorus limitation, suggesting that phosphorus may have been limiting primary production.

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General Introduction

Primary production forms the base of aquatic food webs in river ecosystems (Odum, 1956; Murphy, 2001). The food webs of many rivers that support fish populations contain aquatic macroinvertebrates as an intermediary between basal resources and fish (Murphy, 2001). Therefore, a comprehensive study of the limiting factors controlling juvenile salmon populations should include an examination of possible bottom-up controls, including the influence of environmental variables on basal resources and the influence of those basal resources on aquatic macroinvertebrates. Previous research has shown that studying a river ecosystem at all trophic levels in order to evaluate community-wide changes and effects can shed light on the effects of basal food web resources (Slavik *et al.*, 2004).

River ecosystem metabolism, the combination of in-stream primary production and ecosystem respiration, provides a measure of how much energy is available within a river, and how much energy is used in a river. Energy production in rivers occurs through photosynthetic activity on the part of algae, aquatic plants, and mosses and liverworts. Energy use within rivers occurs through the respiration of all living organisms in the river (Young, Matthaei & Townsend, 2008). Estimates of river primary production and respiration rates can give an indication of the amount of energy available at the base of the food web. They can also be used as a functional indicator of river health (Young *et al.*, 2008). Because river ecosystem metabolism rates can be influenced by environmental variation, including variation in light availability (Young & Huryn, 1996; Acuña *et al.*, 2004), river discharge rates (Acuña *et al.*, 2004; Izagirre *et al.*, 2008), and nutrient concentrations (Guasch, Marti & Sabater, 1995; Young & Huryn, 1999; Mulholland *et al.*, 2001; Slavik *et al.*, 2004; Uehlinger, 2006), it is important to gather baseline estimates of metabolism rates under a variety of environmental conditions.

Environmental variables, particularly extreme hydrologic events, may have direct effects on aquatic macroinvertebrates (Konrad, Brasher & May, 2008); they may also indirectly affect macroinvertebrates via bottom-up effects traveling up through the food

web. For example, macroinvertebrate abundance increases with measured increases in chlorophyll *a*, an indication of algal biomass (Hawkins & Sedell, 1981). Primary producers are a major food source for aquatic macroinvertebrates (McCutchan & Lewis, 2002; Fuller, Kennedy & Nielsen, 2004), which, in turn, are one of the main food sources for juvenile salmon (Loftus & Lenon, 1977; Wipfli, 1997).

This project was undertaken as part of a larger study on the ecological interactions and demographics of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) on an interior Alaskan river. The goal of this larger study was to improve the current understanding of the way ecological processes regulate population size and generate annual variability in the abundance of Chinook salmon in the Chena River, a tributary of the Tanana and Yukon Rivers in interior Alaska. To better understand the controls on juvenile salmon production, it is necessary to determine the availability and dynamics of food resources, including direct sources, such as macroinvertebrates, and indirect sources, such as primary production. The work described here provides a more complete understanding of juvenile Chinook salmon ecology and population dynamics, and river ecology, by illuminating the relationships between environmental variation, ecosystem metabolism (primary production and ecosystem respiration), and benthic macroinvertebrates in the Chena River.

We employed a single-station diel oxygen method (Odum, 1956) and the nighttime regression method (Kosinski, 1984) for estimating river ecosystem metabolism rates at four sites in the Chena River throughout the summers of 2008 and 2009. We also monitored underwater photosynthetically active radiation level, river nutrient concentrations, and discharge rate. In addition, we measured benthic macroinvertebrate densities using a Surber sampler.

The goal of the work described here was to address the relationships between environmental variables and ecosystem metabolism (primary production and ecosystem respiration) in the Chena River, as well as the relationships between these variables and benthic macroinvertebrate densities. Elucidating these relationships allows for a greater understanding of the basal food resources that ultimately support juvenile salmon and

other fishes, as well as provides a baseline for future work involving river ecosystem metabolism and benthic macroinvertebrate densities in the Chena River.

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Chapter 1. Relationships between ecosystem metabolism, benthic macroinvertebrate densities, and environmental variables in a sub-arctic Alaskan river[1]

SUMMARY

1. The aim of this study was to investigate the environmental drivers of river ecosystem metabolism and macroinvertebrate density in a sub-arctic river. Ecosystem metabolism (the combination of gross primary production and ecosystem respiration within a river reach) estimates can indicate how much energy is available and used within a river. Aquatic macroinvertebrates provide a link between the energy produced at the base of the food web and secondary consumers. The extent to which light intensity, discharge rate, and nutrient concentrations influence metabolism rates, and in turn how primary production and river discharge rates influence benthic macroinvertebrate densities in sub-arctic rivers is largely unknown. These processes ultimately help regulate prey resources available for upper level consumers such as juvenile salmon.

2. We employed Random Forests model analyses to identify important predictor variables for primary production and respiration rates (estimated using a single-station diel oxygen method) at four sites in the Chena River, sub-arctic Alaska, throughout the summers of 2008 and 2009. In order to determine the importance of nutrient concentrations, we calculated Spearman correlations between nutrient levels and metabolism rates. We also used Random Forests models to identify the variables important for predicting benthic macroinvertebrate density and biomass in the river.

3. Random Forests models indicated that discharge and length of time between high water events were the most important factors measured for predicting metabolism rates. Discharge was also identified as the most important variable for predicting benthic macroinvertebrate density and biomass.

[1] Benson, E. B., M. S. Wipfli, J. E. Clapcott, and N. F. Hughes. Relationships between ecosystem metabolism, benthic macroinvertebrate densities, and environmental variables in a sub-arctic Alaskan river. Prepared for submission to Freshwater Biology.

4. Phosphorus concentration was low throughout the summers, while nitrogen concentration was more variable; the ratio of nitrogen to phosphorus was above the threshold for phosphorus limitation, suggesting that phosphorus may have been limiting primary production.
5. Our results indicate that the environmental variables we studied in this sub-arctic river have an impact on metabolism rates and benthic macroinvertebrate densities. Primary production and benthic macroinvertebrate density and biomass were negatively related to high flows. Low phosphorus concentration further indicated nutrients may also play a role in regulating basal food resources in this sub-arctic river.

Introduction

Sub-arctic Alaskan rivers are seasonally dominated by a large biomass of primary producers and consumers in the summer months (Oswood *et al.*, 1992). Understanding this seasonal food web, which supports salmon and other upper-level consumers (Oswood *et al.*, 1992), requires knowledge of the basal food supply. Ecosystem metabolism, a combination of gross primary production and ecosystem respiration, plays a major role in regulating these basal food resources in riverine ecosystems (Odum, 1956). In-stream primary production provides a source of energy to grazing invertebrates, and estimates of gross primary production provide measures of the rate at which this energy is made available to them. Conversely, ecosystem respiration reflects the in-stream use of energy, and estimates of the rate of respiration are measures of the rate at which energy is used. Therefore, river ecosystem metabolism rates give an indication of the amount of energy available at the base of the food web (Young, Matthaei & Townsend, 2008).

Environmental variables, including light level, discharge rate, and nutrient availability, can influence metabolism rates in rivers (Young *et al.*, 2008). Underwater light level, a function of riparian vegetation, cloud cover, angle of incident radiation, turbidity, and water depth, can limit primary production in rivers (Young & Huryn,

1996). However, it is not clear the degree to which daily light variation affects primary production rates in sub-arctic river systems exposed to long day-lengths, such as the ecosystem where we conducted this study, where day-lengths can reach 22 hours at mid-summer. The increased light availability that exists at high latitudes may result in increased primary production rates at high latitudes; conversely, primary production rates may be similar to those at lower latitudes if light saturation occurs.

River discharge can affect primary production and respiration rates through a number of mechanisms, including changes in nutrient concentrations and light availability, as well as physical scouring of the riverbed which results in the removal of detritus, microbes, and algal biomass (Young *et al.*, 2008). High flows may bring with them an influx of nutrients (Stevenson, 1990), which may lead to increased primary production and respiration rates if nutrients are limiting. However, high flow can increase turbidity and thus decrease light penetration, which may lead to a decrease in primary production rate (Izagirre *et al.*, 2008). High flows also increase physical scouring of algal communities on the riverbed, which can lead to a decrease in primary production rate (Young *et al.*, 2008). Increased water velocity due to high flows may also lead to a decrease in respiration rate by disrupting microbial activity through scouring and flushing of microbes and the detritus they consume (such as leaf litter and decaying salmon carcasses). Thus, intermediate river flows that balance nutrient inputs, light limitation, and physical scouring and flushing may lead to the highest rates of primary production and respiration.

Nutrient availability may also affect metabolism rates; both primary production and respiration rates can increase in response to nutrient inputs in agricultural streams (Young & Huryn, 1999), and respiration rate has been shown to decrease in response to a decline in nutrient inputs from a sewage treatment facility (Uehlinger, 2006), suggesting that nutrient concentrations may be an important driver of metabolism rates. Most river metabolism studies that have found a relationship between nutrient availability and metabolism rates have relied on settings where nutrient concentrations were affected by human activities, both at high (Slavik *et al.*, 2004) and low (Guasch, Marti & Sabater,

1995; Mulholland *et al.*, 2001; Uehlinger, 2006) latitudes. It is not clear whether metabolism rates also respond to the natural variation in nutrient concentrations that occur in more pristine, high-latitude river ecosystems (but see Betts & Jones (2009) for a discussion of increased metabolism rates following wildfire in a small, sub-arctic Alaskan stream, perhaps due to the mobilization of labile organic matter and nutrients).

Aquatic macroinvertebrates are an important link in river ecosystems between resources at the base of the food web and secondary consumers such as juvenile salmonids and other fishes (Murphy, 2001). Environmental factors can affect aquatic macroinvertebrates directly; they may also, however, have indirect effects on macroinvertebrates by influencing primary producers, one of the main food sources for macroinvertebrates (McCutchan & Lewis, 2002; Fuller, Kennedy & Nielsen, 2004). Macroinvertebrate abundance increases with measured increases in chlorophyll *a*, suggesting that macroinvertebrate abundance may also be related to primary production rate; but this is not always the case (Hawkins & Sedell, 1981).

In addition to indirectly influencing aquatic macroinvertebrates through food web processes, environmental conditions may also directly affect macroinvertebrate abundance. For example, extreme hydrologic events, such as floods and droughts, typically result in reduced benthic macroinvertebrate abundance (Konrad, Brasher & May, 2008). In the case of flooding, as water velocity increases, hydraulic stress may force benthic macroinvertebrates to drift, resulting in lower local benthic densities.

The aim of this study was to investigate the environmental drivers of river ecosystem metabolism and macroinvertebrate density in a sub-arctic river. To address this aim we asked two main questions, with five associated hypotheses. Question one: changes in ecosystem metabolism (primary production and respiration rates) are related to changes in light intensity, river discharge, and nutrient concentrations (Young *et al.*, 2008); of these factors, which is the best predictor of metabolism, and what is the nature of the relationship between each one and metabolism rates? Because light levels often limit primary production (Young & Huryn, 1996), we hypothesized that primary production is highest on days with the greatest light intensities, while ecosystem

respiration rate is largely independent of changes in light intensity, despite the long day-lengths at high latitudes. We also hypothesized that both primary production and ecosystem respiration rates are highest during intermediate river discharge, which balances the countering effects of increased nutrient inputs and increased riverbed scouring and light limitation, all of which are associated with high discharge rates (Stevenson, 1990; Izagirre *et al.*, 2008; Young *et al.*, 2008), and that primary production and ecosystem respiration rates are highest when nutrient concentrations are highest. Question two: changes in benthic macroinvertebrate densities and biomass are likely related to changes in primary production and river discharge; of these factors, which is the best predictor of benthic macroinvertebrate density and biomass, and what is the nature of the relationship between each one and benthic macroinvertebrate density? Because benthic macroinvertebrates rely on primary producers as a major food source (McCutchan & Lewis, 2002; Fuller *et al.*, 2004), we hypothesized that their densities and biomass are greatest during and immediately following periods of high primary production. We also hypothesized that their densities are lowest during and immediately following high river discharges.

We conducted this study on the Chena River in interior Alaska, USA. This is an ideal setting for investigating questions pertaining to ecosystem metabolism and benthic macroinvertebrates in a high-latitude river. The Chena River is located in the sub-arctic region of Alaska, has a natural flow regime, and is virtually free of human development along most of its length.

Methods

Study area

The Chena River is a sixth-order, clear-water river that flows 241 km from its headwaters in the foothills west of Fairbanks, Alaska, to the confluence with the Tanana River, a tributary of the Yukon River. The watershed is approximately 5,200 km^2 and includes

five major tributaries: North Fork, West Fork, South Fork, East (Middle) Fork, and Little Chena River (Fig. 1). Since 1968, mean annual discharge at the U.S. Geological Survey (USGS) Two-Rivers gauging station, located 145 km upstream of the mouth of the river, has been approximately 20 m^3s^{-1} and daily mean flows have ranged from 0.6 to over 496 m^3s^{-1}. Peak discharge typically occurs in early summer, though high flow can occur at any time the river is free of ice. Urban development exists along the lower 40 km of the river, while the upper portions remain relatively undeveloped.

We worked at four study sites located within the middle section of the river, an area roughly 75 km long that supports the majority of the juvenile salmon that rear in the river during the summer (M. Wipfli, unpubl. data). The upper two sites, Site 1 and Site 2, were located 131 km upstream of the mouth of the river (N 64 53.909′, W 146 38.271′) and 123.5 km upstream of the mouth of the river (N 64 52.847′, W 146 43.360′), and the lower two sites, Site 3 and Site 4, were located 88 km upstream of the mouth of the river (N 64 49.052′, W 147 06.273′) and 84 km upstream of the mouth of the river (N 64 48.253′, W 147 07.901′) (Fig. 1). Sites were selected based on accessibility and suitability for sampling techniques; we selected sites that included a long run where we could deploy a data logger just upstream of a riffle big enough to allow for sampling of benthic macroinvertebrates using a Surber sampler.

Sampling regime

We sampled river water and benthic macroinvertebrates at the four study sites once every other week when the river was free of ice from June through late September in 2008, and from May through mid-September in 2009. Thus, there were eight sampling dates per study reach in 2008 and ten sampling dates per study reach in 2009. Continuous data loggers were maintained at all four sites throughout the study periods each year.

Environmental variables

We measured water temperature, turbidity, and photosynthetically active radiation (PAR) using Hydrolab® DS5 Water Quality Multiprobe data loggers (Hach Environmental, Loveland, Colorado, USA). The data loggers recorded an instantaneous reading for each parameter every 15 min during deployment, from which we computed daily means. PAR data was limited to Site 1, Site 3, and Site 4 in 2008 and Site 2 and Site 3 in 2009; thus, we averaged PAR data among those sites, and used the mean of the site values for each day in our subsequent data analyses. Though this meant that there was no inter-site variation in the PAR data, the day-to-day variation in PAR values exceeded the variation in PAR values between sites (data not shown). High flows limited site accessibility at times, and that, along with equipment failure, meant that the length of data logger deployment time varied between years and among sites, but was commonly between 60 and 115 days (see Fig. 2 for an indication of logger deployment times).

To prevent data loggers from becoming damaged during deployment, we wrapped each one in flexible packaging foam and placed it inside a custom-built protective case that consisted of an aluminum pipe set into a five-gallon pail filled with cement, which was anchored to the river bed. We anchored each case approximately two meters from the river bank and in about one meter of water.

Data loggers were maintained every other week by removing the data logger from its case, cleaning off any debris, macroinvertebrates, and biofilm, downloading data files, changing batteries, and re-calibrating the loggers. The data loggers were not re-calibrated after June in 2008 because the calibration procedure did not appear to be working correctly. In 2009, the data loggers were re-calibrated in the field every other week. None of the data loggers exhibited data-drift in a consistent direction throughout the summer in 2009. It is likely that data-drift was similarly unbiased in direction in 2008,.

Mean daily discharge for each site was obtained from the nearest USGS gauging station. We also calculated the time since last high water event as a second discharge metric. A high water event was defined as flow greater than or equal to 50 m^3s^{-1}. This

value was chosen based on visual inspection of hydrographs from past years; we determined that using this threshold would typically result in the occurrence of four to five "high water events" per year in the Chena River. Dates directly prior to high water events when the hydrograph was already starting to rise were not included in the time since last high water event as these days were considered the preliminary days of the next high water event.

We collected one water sample at each site every other week. Water samples were filtered through 0.7-μm Whatman glass microfibre filters and stored in high-density polyethylene (HDPE) bottles in a cooler in the field; they were frozen upon return to the lab. Water chemistry analysis was performed by the Cooperative Chemical Analytical Laboratory at Oregon State University, Corvallis, Oregon, USA using APHA methods (APHA, 2005). Water samples were analyzed for dissolved soluble reactive phosphorus (SRP; detection limit: 0.001 mg L^{-1}), dissolved nitrate plus nitrite (NO_3^--N + NO_2^--N; detection limit: 0.001 mg L^{-1}), dissolved ammonia (NH_4^+-N; detection limit: 0.010 mg L^{-1}), and dissolved organic carbon (DOC; detection limit: 0.05 mg L^{-1}). The ratio of nitrogen to phosphorus (N:P) was calculated as the atomic ratio of NO_3^--N + NO_2^--N + NH_4^+-N to SRP.

Ecosystem metabolism

We estimated ecosystem metabolism rates at 15-min intervals at each site using a single-station diel oxygen method (Odum, 1956), and subsequently calculated daily mean metabolism rates. Dissolved oxygen concentration and percent saturation were recorded at 15-min intervals by data loggers (see previous section). We used these data, together with the temperature data recorded at the same time, to estimate daily mean gross primary production and ecosystem respiration, using the night-time regression technique (Marzolf, Mulholland & Steinman, 1994, 1998; Young & Huryn, 1998). Metabolism estimates were made using a spreadsheet entitled "Microsoft® Excel model to calculate ecosystem metabolism", which is available from the Cawthron Institute in Nelson, New

Zealand (http://www.cawthron.org.nz/coastal-freshwater-resources/downloads.html). Estimates of gross primary production rate were made at 15-min intervals using a derivative of the following equation:

$$dO/dt = \text{GPP} - \text{ER} - (k*D) \quad \text{[Eq. 1]}$$

Where dO/dt is the rate of change in dissolved oxygen concentration ($gO_2\ m^{-3}\ sec^{-1}$), GPP is gross primary production ($gO_2\ m^{-3}\ sec^{-1}$), ER is ecosystem respiration ($gO_2\ m^{-3}\ sec^{-1}$), k is the reaeration coefficient (sec^{-1}), and D is the oxygen deficit (or surplus) in the river (i.e., the difference between the measured oxygen concentration and the value at 100% saturation; $gO_2\ m^{-3}$). We measured dissolved oxygen concentration and calculated the oxygen deficit based on those measurements and simultaneous measurements of temperature. We employed the night-time regression technique to estimate ecosystem respiration rate and the reaeration coefficient.

The night-time regression technique allows one to estimate reaeration and ecosystem respiration from the oxygen concentrations recorded in the dark; during the night-time, the change in oxygen concentration over time is equal to the product of the reaeration coefficient and the oxygen deficit, plus the rate of respiration. Thus, by regressing the change in oxygen concentration over time against the oxygen deficit, it is possible to estimate the reaeration coefficient (the slope of the regression line), and the respiration rate (the y-intercept of the regression line). This technique assumes that respiration and reaeration are constant across the day and night (Kosinski, 1984; Young & Huryn, 1996).

We validated night-time regression estimates (and the assumption that night length was long enough to enable the use of this technique at a sub-arctic latitude) using a day-time regression technique (Kosinski, 1984) on a selection of data. The day-time regression technique is similar to the night-time regression method in that one can estimate reaeration and respiration rate by using the oxygen record to build a regression; it is different in that it requires above-canopy photosynthetically active radiation (PAR) data, because primary production is assumed to be a function of light level (Kosinski, 1984). We used PAR data collected by the University of Alaska Fairbanks at Poker Flat

Research Range (N 65 7.080′, W 147 25.920′; about 50 km from study sites), and stored by the UV-B Monitoring and Research Program of the United States Department of Agriculture (http://uvb.nrel.colostate.edu/UVB/da_queryPar.jsf) to approximate above-canopy PAR at our study sites on the Chena River. We also verified that possible relationships between metabolism rates and river discharge rate were not simply an artifact of reaeration changing with discharge by calculating the Spearman correlation between the reaeration coefficient and river discharge rate.

Metabolism estimates were calculated in volumetric units and converted to areal units by multiplying primary production and respiration rates by mean reach depth. We measured mean reach depth at each site on four or five dates throughout the 2008 field season by taking five measurements across each of five transects located above each site. We estimated mean reach depth for each day throughout the field seasons at each site by regressing mean reach depth measurements against discharge rates reported by the USGS gauging station closest to each site. We used the 2008 regressions to estimate daily mean reach depths in 2008 and 2009.

We calculated the mean daily primary production estimates at each site for the week prior to benthic macroinvertebrate sampling to use in the benthic macroinvertebrate analysis.

Benthic macroinvertebrates

We collected two replicate benthic macroinvertebrate samples from riffle habitat at each site every other week, except when we were unable to because of high water. We collected the samples with a 500-μm, 0.1 m^2 Surber sampler and preserved them in the field in 80% ethanol. In the lab, we sorted, counted, measured (to the nearest 0.5 mm), and identified (to family) the macroinvertebrates. We estimated their biomass via published length-weight regressions (Uye, 1982; Meyer, 1989; Burgherr & Meyer, 1997; Kawabata & Urabe, 1998; Benke *et al.*, 1999; Johnson & Strong, 2000; Sabo, Bastow & Power, 2002; Baumgartner & Rothhaupt, 2003; Gruner, 2003; Miyasaka *et al.*, 2008; M.

Wipfli, unpubl. data). We calculated the mean benthic macroinvertebrate density and biomass between replicate samples.

In addition to our broader benthic macroinvertebrate data analyses (described below), we tested for relationships between benthic Heptageniidae density, as well as benthic Heptageniidae biomass, and the rate of gross primary production during the week prior to benthic macroinvertebrate sampling. We chose to use Heptageniidae density and biomass as an indicator of scraper density and biomass, as this functional feeding group is most likely to rely on algae as a major food source (Cummins, Merritt & Berg, 2008). Of the families we observed in our benthic macroinvertebrate samples, Heptageniidae was the only one in which most members are scraping macroinvertebrates (Waltz & Burian, 2008); all other families we observed that include scrapers also include members of other functional feeding groups as well. It was also one of the taxa present in the majority of our samples.

Data analysis

Random Forests is a statistical modeling method that can be used for regression analyses to describe relationships between variables (Breiman, 2001; Cutler *et al.*, 2007). Output includes partial dependence plots, which are x-y plots that display the predicted relationship between two variables after removing the effects of the other variables included in the model (Elith, Leathwick & Hastie, 2008). Partial plots represent the predicted relationship between two variables, rather than the actual relationship; thus, care should be taken when interpreting them as they may appear to over-state confidence in the depicted relationship. We chose to use this statistical approach instead of a more traditional technique such as generalized linear models because the environmental variables in our study were highly collinear (data not shown). High collinearity violates one of the key assumptions of linear modeling; Random Forests, however, has no such assumption (Cutler *et al.*, 2007). To develop our Random Forests models, we used the R program RFmodelSel, which was designed for building Random Forests classification or

regression models. The regression model selection criteria in this program are: greatest percent variation explained, smallest mean squared error, and smallest number of parameters (Murphy, Evans & Storfer, 2010).

We log-transformed the primary production data to improve the symmetry of their distribution; the transformation normalized the data and reduced clumping. The rest of the metabolism data did not require transformation. The metabolism models included PAR, turbidity, temperature, discharge, days since last high water event, ordinal date, year, and site as possible predictor variables. We also developed alternative metabolism models that did not include year and site as possible predictor variables (though they did include all other variables listed above). These metabolism models were developed simply to determine how much variation in the metabolism data was explained by the environmental variables alone.

We used two-sided Spearman correlations to test for relationships between nutrient concentrations and metabolism metrics instead of including the nutrient data in the Random Forests models. We used this approach because we had daily nutrient concentrations for eight dates in 2008 and ten dates in 2009 rather than daily concentrations throughout the field seasons. We also used two-sided Spearman correlations to test for relationships between benthic Heptageniidae density, as well as benthic Heptageniidae biomass, and the rate of gross primary production during the week prior to benthic macroinvertebrate sampling.

We developed separate Random Forests models for benthic macroinvertebrate density and biomass. We included primary production rate, discharge, ordinal date, year, and site as possible predictor variables in initial models, but in the final versions we only included discharge, ordinal date, year, and site. We left primary production rate as a possible predictor variable out of the final models because it was not identified as an important predictor variable in the original models and because doing so allowed us to include dates that were missing primary production rates in the data analysis.

We conducted all analyses using R, a free statistical package available online (R Development Core Team, 2008).

Results

Environmental variables

Environmental conditions (water temperature, turbidity, photosynthetically active radiation, and river discharge) were similar among the study sites, but varied between years; in particular, water temperature and photosynthetically active radiation were higher in 2009, while river discharge was lower (Table 1).

In both 2008 and 2009, NH_4^+-N and SRP concentrations were low (at times below the detection limits), while NO_2^--N+NO_3^--N and DOC concentrations were more variable throughout the summer (Fig. 3). For dates when SRP was detectable, N:P ratios ranged from 33:1 to 172:1 in 2008, and from 27:1 to 143:1 in 2009.

Ecosystem metabolism

Pearson's correlations showed that both the night-time and day-time regression techniques for estimating metabolism rates produced highly correlated estimates (primary production: Pearson $r = 0.90$, $n = 370$, $P < 0.001$; ecosystem respiration: Pearson $r = 0.63$, $n = 370$, $P < 0.001$; appendix A), but we chose to report night-time regression estimates in order to include our full data-set in our analyses rather than just the sub-set. Metabolism rates were significantly higher when estimated using the night-time regression technique, by 0.07 g O_2 m^{-2} day^{-1} for primary production, and by 1.03 g O_2 m^{-2} day^{-1} for ecosystem respiration (primary production: paired $t(369) = -3.76$, $P < 0.001$; ecosystem respiration: paired $t(369) = -7.12$, $P < 0.001$). A two-sided Spearman correlation showed that reaeration coefficient value was not correlated with river discharge rate ($n = 539$, $\rho = -0.047$, $P = 0.274$; Appendix B).

River ecosystem metabolism rates were variable throughout the two field seasons and between sites, but in general both primary production and ecosystem respiration rates were higher at Site 1 than at the other three study sites (Fig. 2; Table 2). The variables

included in the Random Forests model for primary production explained 75% of the variance in the data, and the model identified site as the overall most important variable, followed by discharge. Turbidity, photosynthetically active radiation (PAR), ordinal date, year, and temperature were approximately equal in importance, and the final variable that the model identified was time since last high water event (Fig. 4a). The variables included in the alternative Random Forests model for primary production (i.e. the model that did not include year and site as possible predictor variables) explained 63% of the variance in the data.

The variables included in the model for respiration explained 52% of the variance in the data, and the model indicated that site was the overall most important variable. Ordinal date, PAR, and time since last high water event were identified as the next most important variables, with approximately equal importance, and temperature was also identified as important (Fig. 4b). The variables included in the alternative Random Forests model for respiration (i.e. the model that did not include year and site as possible predictor variables) explained 31% of the variance in the data.

Photosynthetically active radiation (PAR) was ranked third in importance for predicting primary production rate, along with several other variables; the partial dependence plot for PAR showed that primary production rate had a positive relationship with PAR values below approximately 0.3 $mEs^{-1}m^{-2}$; at PAR intensities above this threshold, primary production rate remained constant (Fig. 5a). In addition, PAR was ranked as the second most important variable for predicting respiration rate, along with two other variables; the partial dependence plot for PAR showed that there was a positive relationship between respiration rate and PAR values below approximately 0.5 $mEs^{-1}m^{-2}$; at PAR values above this threshold, respiration rate remained constant (Fig. 5b).

Discharge was identified as the second most important variable for predicting primary production rate, and the partial dependence plot for discharge showed that primary production rate peaked at intermediate discharge (Fig. 6a). For respiration rate, discharge was not identified as an important predictor. However, time since last high water event, an alternative measure of discharge, was tied with other variables as the

second most important predictor for respiration rate; the partial dependence plot for time since last high water event indicated that respiration rate was lowest at the greatest time since last high water event (Fig. 6b).

Two-sided Spearman correlations, with a family-wise alpha of 0.05 for each year, revealed no significant relationships between metabolism rates and nutrient concentrations in 2008; in 2009, there was a positive relationship between NO_2^--N+NO_3^--N and N:P ($n = 22$, $\rho = 0.897$, $P < 0.001$).

Benthic macroinvertebrates

Benthic macroinvertebrate density and biomass were variable throughout the two field seasons and between sites (Table 2). Chironomidae was the most commonly encountered benthic macroinvertebrate taxon at Sites 2, 3, and 4, in both 2008 and 2009 (representing 60%, 51%, and 45% of individuals at Sites 2, 3, and 4 in 2008, and 42%, 52%, and 53% of individuals in 2009), while Simuliidae was the dominant benthic macroinvertebrate taxon at Site 1 during both years (representing 45% of individuals in 2008, and 31% of individuals in 2009). Other commonly encountered taxa at the four sites included Heptageniidae, Ephemerellidae, Hydracarina, Nemouridae, Chloroperlidae, and Oligochaeta (Table 3).

The variables included in the Random Forests model for benthic macroinvertebrate density explained 58% of the variance in the data, and the model indicated that discharge was the overall most important variable, followed by ordinal date and year, which were approximately equal in importance (Fig. 7a). The variables included in the alternative Random Forests model for benthic macroinvertebrate density (i.e. the model that did not include year and site as possible predictor variables) explained the same amount of the variance in the data (58%). The variables included in the model for benthic macroinvertebrate biomass explained 39% of the variance in the data, and the model identified discharge as the overall most important variable, followed by ordinal date and year, which were approximately equal in importance, and finally by site (Fig.

7b). The variables included in the alternative Random Forests model for benthic macroinvertebrate biomass (i.e. the model that did not include year and site as possible predictor variables) explained 27% of the variance in the data.

Primary production rate was not identified as an important predictor for either benthic macroinvertebrate density or biomass in the preliminary Random Forests models. Two-sided Spearman correlations showed that gross primary production was not correlated with benthic Heptageniidae density ($n = 38$, $P = 0.401$) or benthic Heptageniidae biomass ($n = 38$, $P = 0.693$; Appendix C).

Discharge was identified as the most important variable for predicting benthic macroinvertebrate density, and the partial dependence plot for discharge showed that benthic macroinvertebrate density was lowest at high discharge rates (Fig. 8).

Discussion

Metabolism and photosynthetically active radiation

Primary production rate increased with increasing photosynthetically active radiation (PAR) intensity as expected, and then plateaued as light saturation occurred. We also found an unexpected increase and plateau in respiration rate with increasing PAR intensity. Light availability has been identified as an important factor influencing primary production rate, but it generally does not directly influence respiration rate because processes that contribute to respiration are not necessarily photosynthetic processes (Young *et al.*, 2008). However, respiration rate and light intensity may appear to be related if algae are responsible for a substantial proportion of the respiration occurring in the river, a condition that can occur in well-lit streams and rivers (Bunn, Davies & Mosisch, 1999; Young *et al.*, 2008). Due to its sub-arctic location, the Chena River is abundantly well-lit during the summer months, when our study occurred; thus, a large portion of the respiration occurring in the river may have been due to algal activity.

Metabolism and discharge

Our results supported the hypothesis that primary production rate is greatest at intermediate river flow in the Chena River. Primary production rate was greatest at discharge values between base flow and approximately 28 m^3s^{-1}. At higher discharge rates, primary production rate declined; this was likely because increased flow is associated with increased nutrient inputs (Stevenson, 1990), but also with decreased light availability and increased water velocity. Primary production rate has been shown to decline in response to decreased light availability and increased turbidity (Izagirre *et al.*, 2008), both of which occur during flooding; primary production rate also declines during flooding as a result of reduced algal biomass due to abrasion caused by high water velocity (Young *et al.*, 2008). Intermediate river flow apparently represents a balance between the positive effects of nutrient inputs and the negative effects of decreased light availability and increased water velocity.

We hypothesized that respiration rate is also greatest at intermediate river flow in the Chena River; however, we did not find evidence to support this. In fact, the Random Forests model for respiration did not identify discharge as an important predictor of respiration rate. The model did, however, identify time since last high water event as an important predictor. Respiration rate tended to be greatest at the shortest time since last high water event, and as the time since last high water event lengthened, respiration rate fell. Respiration rate may have been highest directly following a high water event because floods are associated with increased nutrient and organic matter inputs (Stevenson, 1990; Roberts, Mulholland & Hill, 2007).

One of the ways in which discharge affects primary production rate is through abrasion of algal biomass. Abrasion due to high flow typically does not affect respiration rate to the same extent because a substantial portion of respiration can occur in the hyporheic zone, where respiring microbes are protected from abrasion (Fellows, Valett & Dahm, 2001). This may be one explanation for why discharge was not identified as an important predictor of respiration rate in the Chena River. Furthermore, if most respiration occurs in the hyporheic zone and is therefore unaffected by abrasion during

floods, we would expect that respiration rate would not be low directly following a flood (contrary to what we would expect for primary production rate).

Metabolism and nutrients

We did not find any evidence to support our hypothesis that both primary production and respiration rates are highest at greatest nutrient concentrations in the Chena River. We found no relationships between primary production rate and any of the nutrients measured in either year, nor any relationships between respiration rate and any of the nutrients measured in either year.

In our study, we were not aware of any major human-caused increases or decreases in nutrient concentrations throughout the field seasons. We found that NH_4^+-N and SRP concentrations were low throughout the study (at times below the detection limits), while NO_2^--N+NO_3^--N concentration was somewhat higher. In addition, the N:P ratios were well above the threshold for phosphorus limitation (Cai *et al.*, 2008), suggesting phosphorus may have been one of the factors limiting metabolism in the Chena River.

If phosphorus was limiting metabolism, any available phosphorus would have been taken up by primary producers immediately, and therefore no longer be detectable in the water. This could explain why we did not find a correlation between metabolism rates and soluble reactive phosphorus (SRP) concentration; if phosphorus was taken up immediately upon becoming available, SRP inputs to the river would not have been reflected in water samples. In addition, if phosphorus, rather than nitrogen, was limiting metabolism, then metabolism rates would not have responded to variation in nitrogen concentration in the river. Although we observed moderate changes in NO_2^--N+NO_3^--N concentration throughout the field seasons, we did not find any correlations between metabolism rates and NO_2^--N+NO_3^--N, suggesting that nitrogen was always available in abundance relative to phosphorus.

Our results suggest that phosphorus, rather than nitrogen, was limiting metabolism in the Chena River, although we did not conduct nutrient-limitation studies; this is consistent with the results of a study on nutrient concentrations in the Chena River conducted in 2005-2006 (Cai *et al.*, 2008). Long-term phosphorus fertilization of the Kuparuk River, an arctic river on the North Slope of Alaska, resulted in increases in metabolism rates, chlorophyll *a* concentrations, and fish growth rates (Slavik *et al.*, 2004), suggesting that phosphorus was one of the factors limiting primary production, with effects that transferred up through the food web and affected multiple trophic levels.

Benthic macroinvertebrates and primary production rates

Our results did not support the hypothesis that benthic macroinvertebrates are more abundant and larger during or following periods of the highest rates of primary production in the Chena River. We expected that benthic macroinvertebrates would be more abundant and their biomass would increase following periods of high primary production because algal activity drives primary production rate and is an important food source for stream macroinvertebrates (McCutchan & Lewis, 2002), but the preliminary benthic macroinvertebrate Random Forests models we ran did not identify primary production as an important variable for predicting benthic macroinvertebrate density or biomass. In addition, two-sided Spearman correlations showed that gross primary production was not correlated with benthic Heptageniidae density or benthic Heptageniidae biomass. This finding suggests that the results of the Random Forests models were not simply an artifact of including all functional feeding groups in the models. Because scraping macroinvertebrates, of which Heptageniidae is one example (Waltz & Burian, 2008), are the functional feeding group most likely to rely on algae as a major food source (Cummins *et al.*, 2008), we expected that this group would be most likely to show a relationship with primary production. However, gross primary production rates were not correlated with either Heptageniidae density or biomass.

One explanation for detecting no relationships between benthic macroinvertebrate density or biomass and primary production rate may be that benthic macroinvertebrate growth responds to changes in primary production rate on an annual scale rather than a seasonal one. Our study included data from only two years, which is not enough time to test such a hypothesis. Past research, however, has indicated that benthic macroinvertebrate density can increase in response to additional food resources in as short as 17 days (Wipfli *et al.*, 1999), suggesting that this explanation is not likely. Studies conducted in Alaska that have found an increase in benthic macroinvertebrate abundance following an increase in food resources (such as a natural salmon spawning event or an experimental salmon carcass addition, which can lead to increased biofilm chlorophyll *a* levels and ash-free dry mass) typically have much greater, and sustained, increases in food resources than we saw naturally occurring in the Chena River during our study (Wipfli, Hudson & Caouette, 1998; Wipfli *et al.*, 1999; Tiegs *et al.*, 2009). This could explain why we did not find a relationship between benthic macroinvertebrates and primary production rate; perhaps an increase in food resources has to be large, as well as sustained, to have an observable affect on benthic macroinvertebrates. However, another explanation may be that a longer time lag than the one we used (i.e. longer than one week) was necessary to observe an effect on benthic macroinvertebrates.

Benthic macroinvertebrates and discharge

We found evidence to support our hypothesis that benthic macroinvertebrates are least abundant during high flows. Our Random Forests model identified discharge as the most important variable for predicting benthic macroinvertebrate density, and the accompanying partial dependence plot showed a negative relationship between benthic macroinvertebrate densities and discharge rates above approximately 20 m^3s^{-1}. Though this rate of flow is well below the threshold of 50 m^3s^{-1} that we used to categorize substantial high water events in our analysis, it appears to be the threshold for ecologically significant floods, at least in the case of benthic macroinvertebrates.

Extreme hydrologic events, such as floods and droughts, typically result in reduced benthic macroinvertebrate abundance (Konrad *et al.*, 2008). In the case of flooding, as water velocity increases, benthic macroinvertebrates are more likely to leave the river bed because of the hydraulic stress they are experiencing. As more benthic macroinvertebrates begin to drift, fewer remain on the river bed (at least in the riffle habitats that we sampled); thus, following high discharge rates that promote drifting, benthic macroinvertebrates are less abundant.

Summary

Our models identified site as the most important variable for predicting primary production and respiration rates. This suggests that there was some environmental factor or factors that differed among the study sites that we were unable to capture in our environmental measurements; in addition, there could have been environmental factors that did not differ among the study sites that we were unable to measure, which could account for the percentage of variation in the data that the models could not explain. During both 2008 and 2009, primary production and respiration rates were substantially higher at the furthest up-river site (Site 1) than at the other three study sites. There are several possibilities that could account for the difference in metabolism rates between Site 1 and the other sites. Site 1 is separated from the other three sites by a major tributary (the South Fork of the Chena River); this separation could lead to ecological differences between the sites that could influence metabolism rates such as differences in pH levels (Niyogi, Lewis & McKnight, 2002; Young *et al.*, 2008), differences in the size and stability of river-bed substrate (Young *et al.*, 2008), or differences in hyporheic connectivity (Fellows *et al.*, 2001), none of which were measured in this study.

Another set of factors that could account for the difference in metabolism rates between our study sites is differences in benthic macroinvertebrate density, biomass, or community composition. Benthic macroinvertebrate density and biomass did not differ between the study sites in the same pattern as the difference in metabolism rates (i.e.

Sites 2, 3, and 4 similar, and all different from Site 1); however, benthic macroinvertebrate community composition did differ in that fashion. Simuliidae was the most common taxon at Site 1 in both years, while Chironomidae was the most common taxon at the other three sites in both years. Members of the Simuliidae family generally belong to the collector-filterer functional feeding group (Adler & Currie, 2008), while members of the Chironomidae family generally belong to the collector-gatherer, collector-filterer, or predator functional feeding groups (Ferrington, Berg & Coffman, 2008). The differences in their methods of collecting food and relative abundance at the study sites could affect the amount and quality of biofilm at the study sites, which in turn may have led to the differences in metabolism rates that we observed.

Another feature that could have influenced metabolism rates at our study sites is spawning salmon. When adult salmon return to their natal streams and rivers to spawn, the result is an influx of marine-derived nutrients in the form of fish carcasses, eggs, and metabolic waste (Tiegs *et al.*, 2009). Our results suggest that phosphorous may have been limiting metabolism in the Chena River; thus, if our study sites experienced different densities of spawning salmon, we would expect those sites with a higher number of spawning salmon to have higher rates of metabolism as well. Aerial surveys conducted during the late summer in 2005 and 2007 indicate that salmon redds, or areas where female salmon deposit their eggs, were more abundant near Site 1 than at locations near our other three study sites (Appendix D); furthermore, the area where redd density peaked was up-river of all of our study sites (S. Decker, unpubl. data). Though the aerial surveys were conducted prior to the present study, the consistency between the two years suggests that salmon redds were likely more abundant near Site 1 than near our other three study sites during the years of our study. The higher rates of metabolism that we observed at Site 1 could have been a result of increased nutrient availability due to the proximity of spawning salmon.

Conclusions

We found that both primary production and respiration rates increased with photosynthetically active radiation (PAR) up to a point, and then leveled off. The relationship between respiration rate and PAR suggests that a substantial portion of the respiration occurring in the Chena River may be due to algae. We also found that metabolism did not increase with increasing nutrient concentrations, perhaps because metabolism may have been limited by phosphorus availability. Primary production rate was highest at intermediate discharge rate, and discharge was the most important variable for predicting primary production rate with the exception of site. Respiration rate was highest directly following high water events, and declined with increasing time since last high water event. Time since last high water event was tied with date and PAR as the second-most important variable for predicting respiration rate, following site.

Though site was most important for predicting metabolism rates, it was not identified as particularly important in our benthic macroinvertebrate models. These models also did not identify periods of high primary production rate as important for increasing benthic macroinvertebrate density and biomass, perhaps because of the lack of periods with a high and sustained rate of primary production during our study. The benthic macroinvertebrate models both indicated that discharge was the most important variable for predicting densities and biomass, and benthic macroinvertebrate density was lowest at the highest discharge rates.

In conclusion, river discharge rate and length of time between high water events were the most important of the environmental factors that we studied for predicting changes in basal food web resources in the Chena River; in addition, our results suggest that phosphorus may have been limiting primary production in the river. These findings have important implications for river management because management schemes invariably cause changes to discharge rates and flow regimes, and added development within a watershed typically increases nutrient loading. The effects of these changes can cascade through the food web of a river through the impact they have on resources at the

base of the food web, such as metabolism rates and benthic macroinvertebrates. In our study, we also found small-scale spatial differences in metabolism rates (differences between study sites on a single river). Conclusively determining which environmental factors are responsible for these differences would be a worthwhile direction for future research.

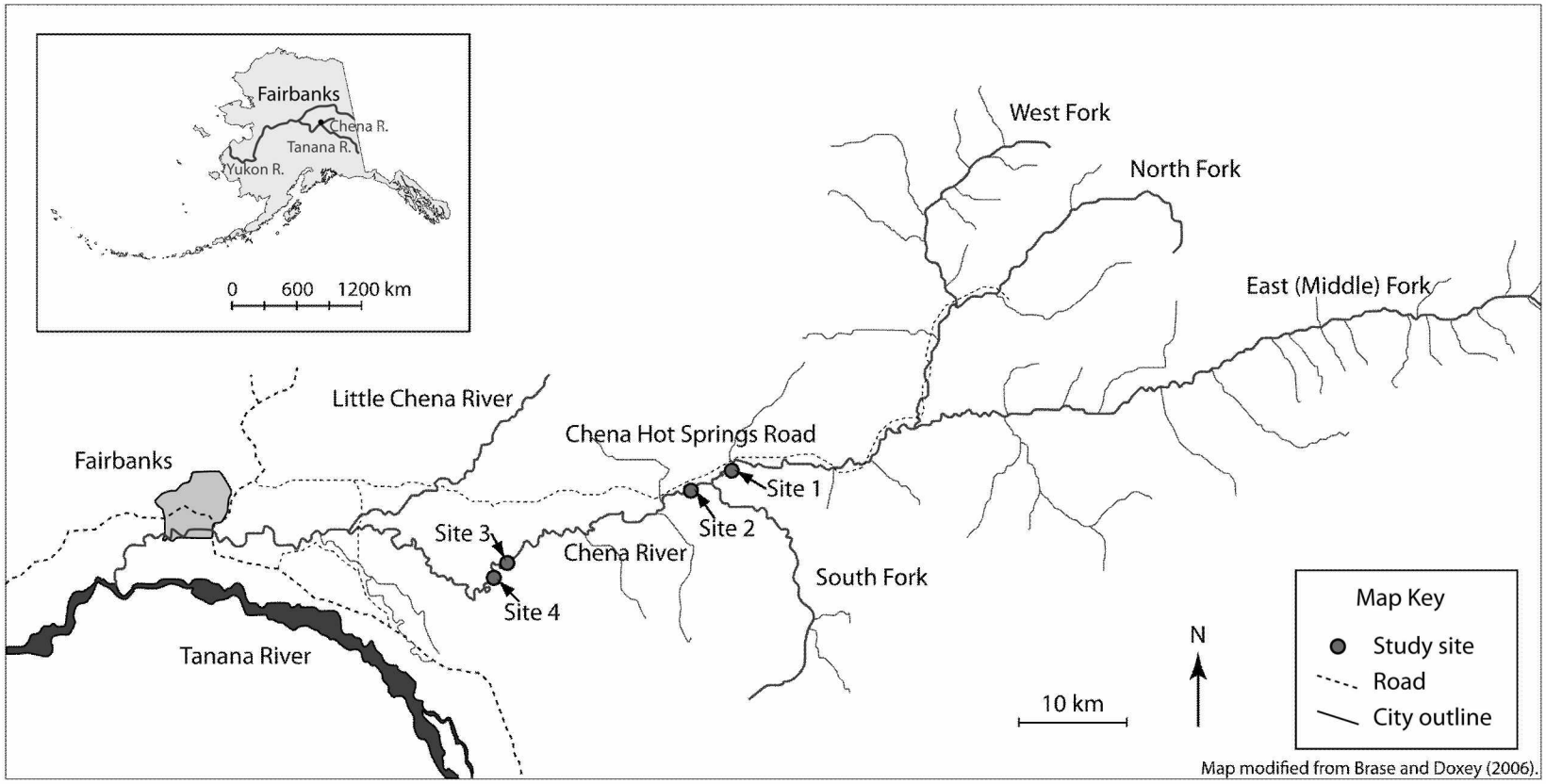

Fig. 1. Location of study sites for investigating ecosystem metabolism, benthic macroinvertebrates, and environmental variation on the Chena River, Alaska, USA, 2008-2009.

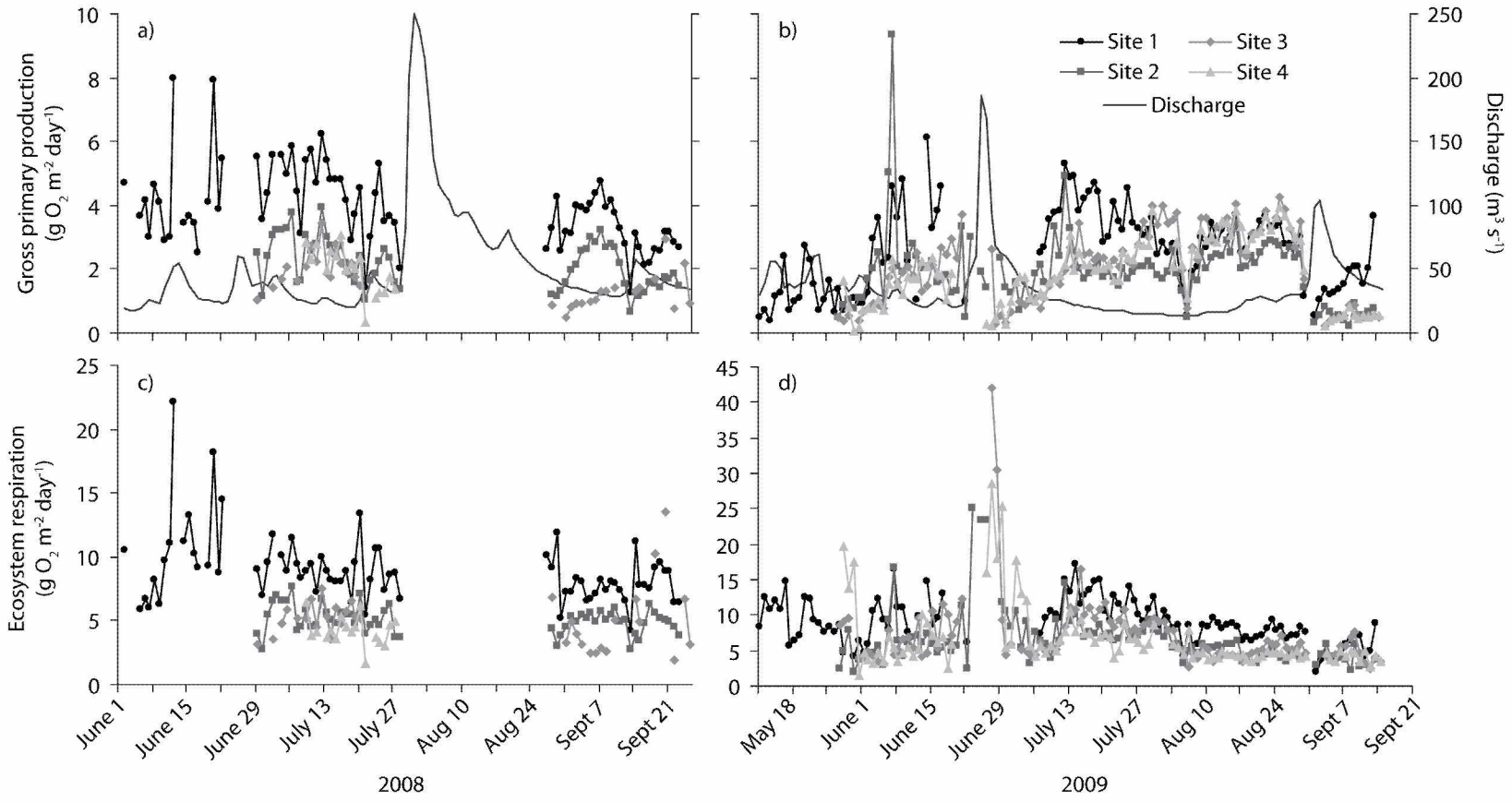

Fig. 2. Gross primary production and river discharge rates in (a) 2008 and (b) 2009, and ecosystem respiration rates in (c) 2008 and (d) 2009 at four sites in the Chena River, Alaska, USA. Gaps represent dates during which data were unavailable due to equipment failure or site inaccessibility.

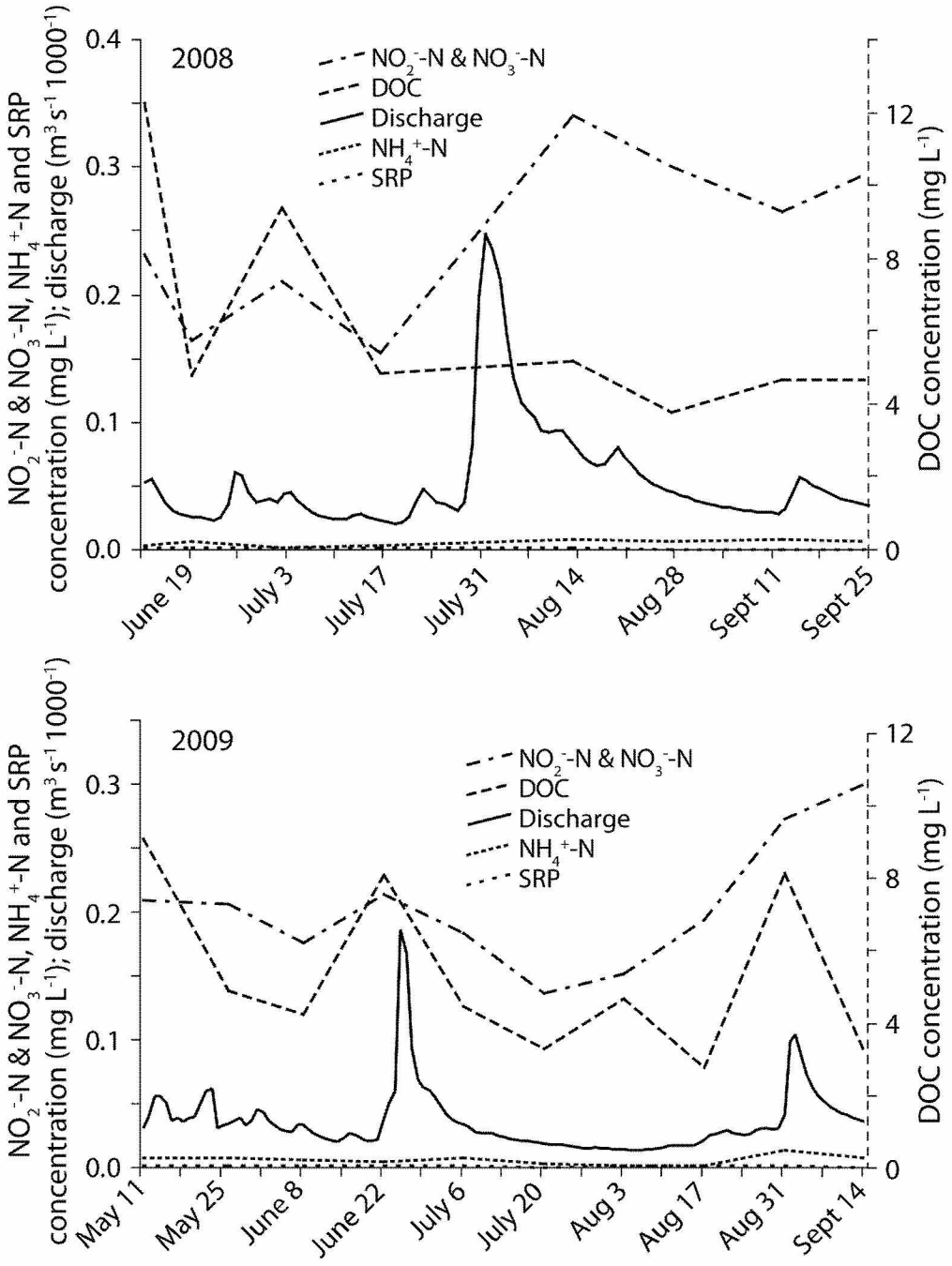

Fig. 3. Nutrient concentrations and mean daily discharge rate in the Chena River, Alaska, USA, throughout the summers of 2008 (upper panel) and 2009 (lower panel). Data are mean values among the four study sites. Nutrients measured include: nitrite and nitrate nitrogen (NO_2^--N and NO_3^--N), ammonia nitrogen (NH_4^+-N), soluble reactive phosphorus (SRP), and dissolved organic carbon (DOC).

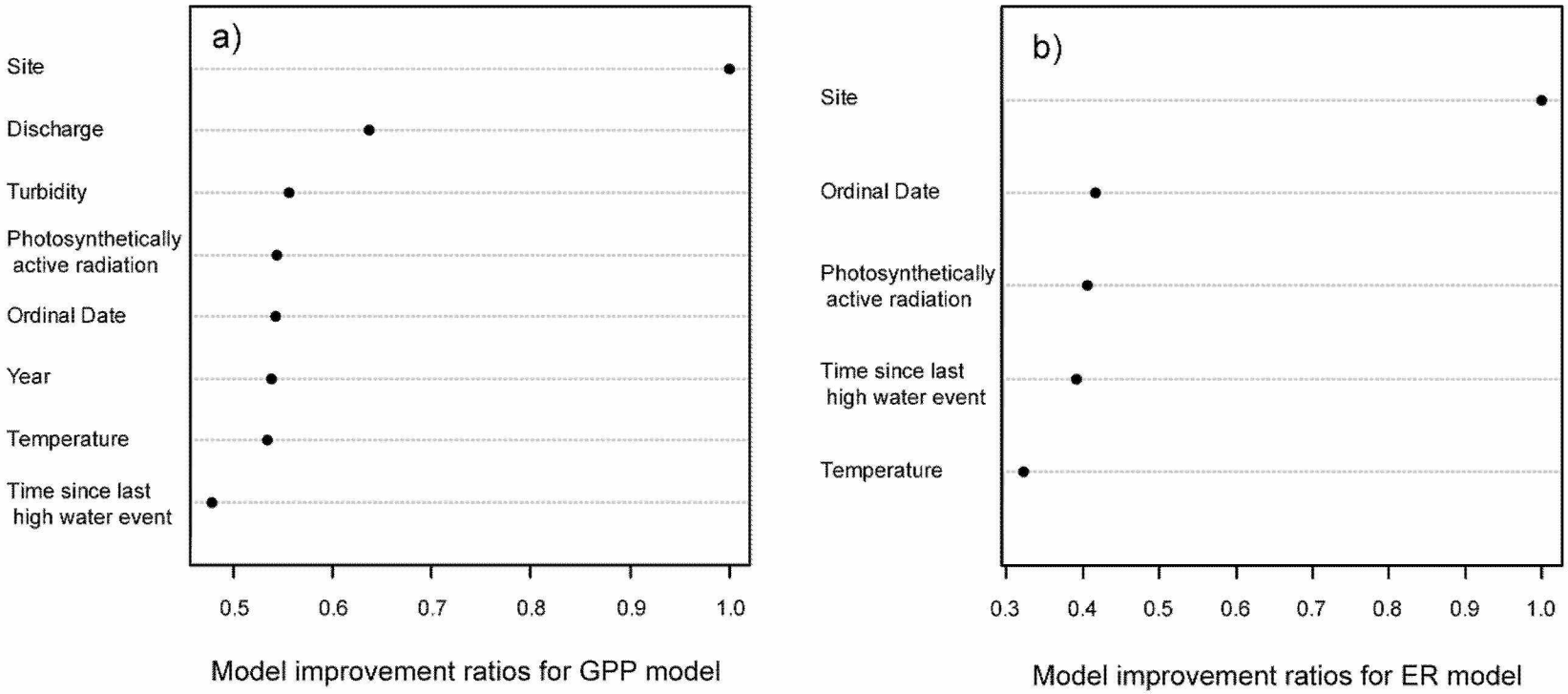

Fig. 4. Model improvement ratios and variable importance rankings for (a) gross primary production rate (GPP) and (b) ecosystem respiration rate (ER) Random Forests models in the Chena River, Alaska, USA, 2008-2009. The primary production model explains 75% of the variation in primary production rates in the Chena River and the respiration model explains 52% of the variation in respiration rates. If site and year are not included as predictor variables in the models, the primary production model explains 63% of the variation in the primary production rates, and the respiration model explains 31% of the variation in respiration rates.

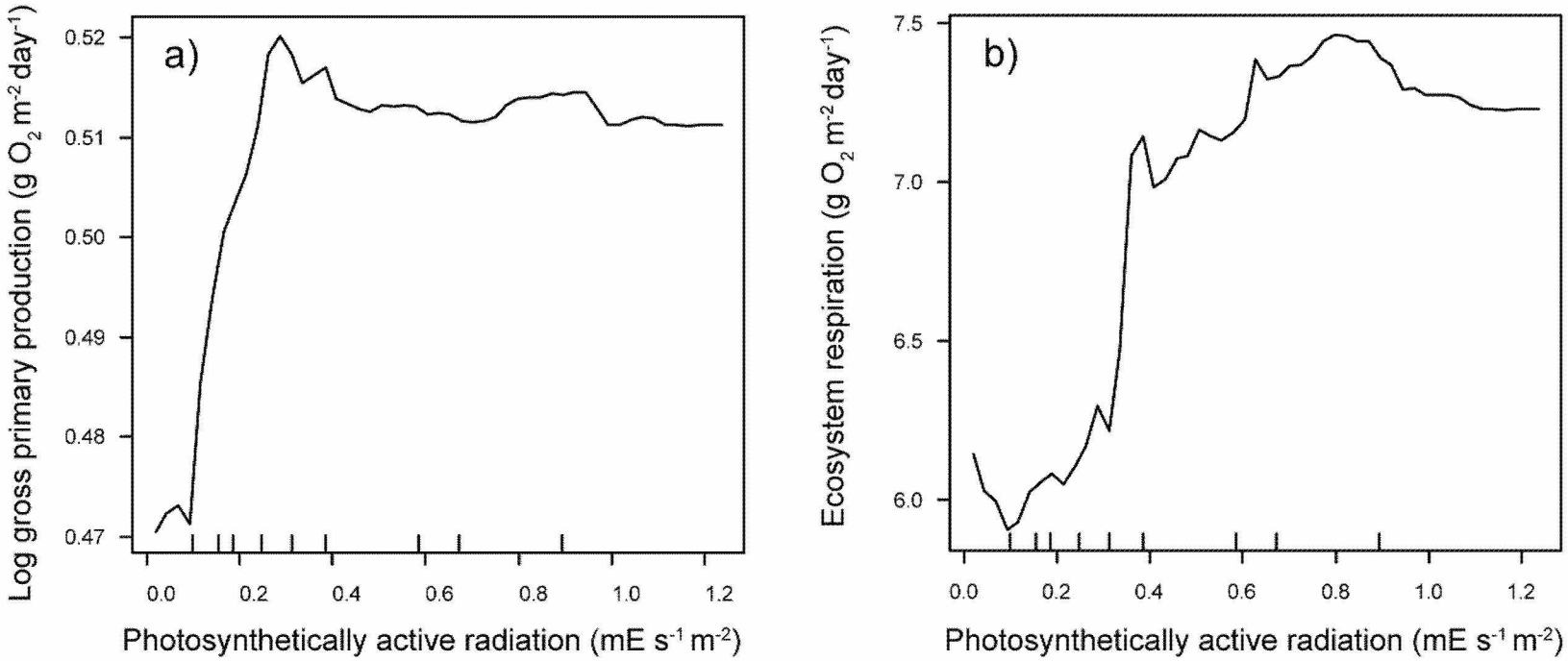

Fig. 5. Effects of photosynthetically active radiation (PAR) on (a) primary production rate and (b) respiration rate in the Chena River, Alaska, USA, 2008-2009. These partial dependence plots show the influence of PAR on primary production rate and respiration rate with the effects of all other variables removed. Inward-facing vertical dash marks on the x-axes represent deciles of data.

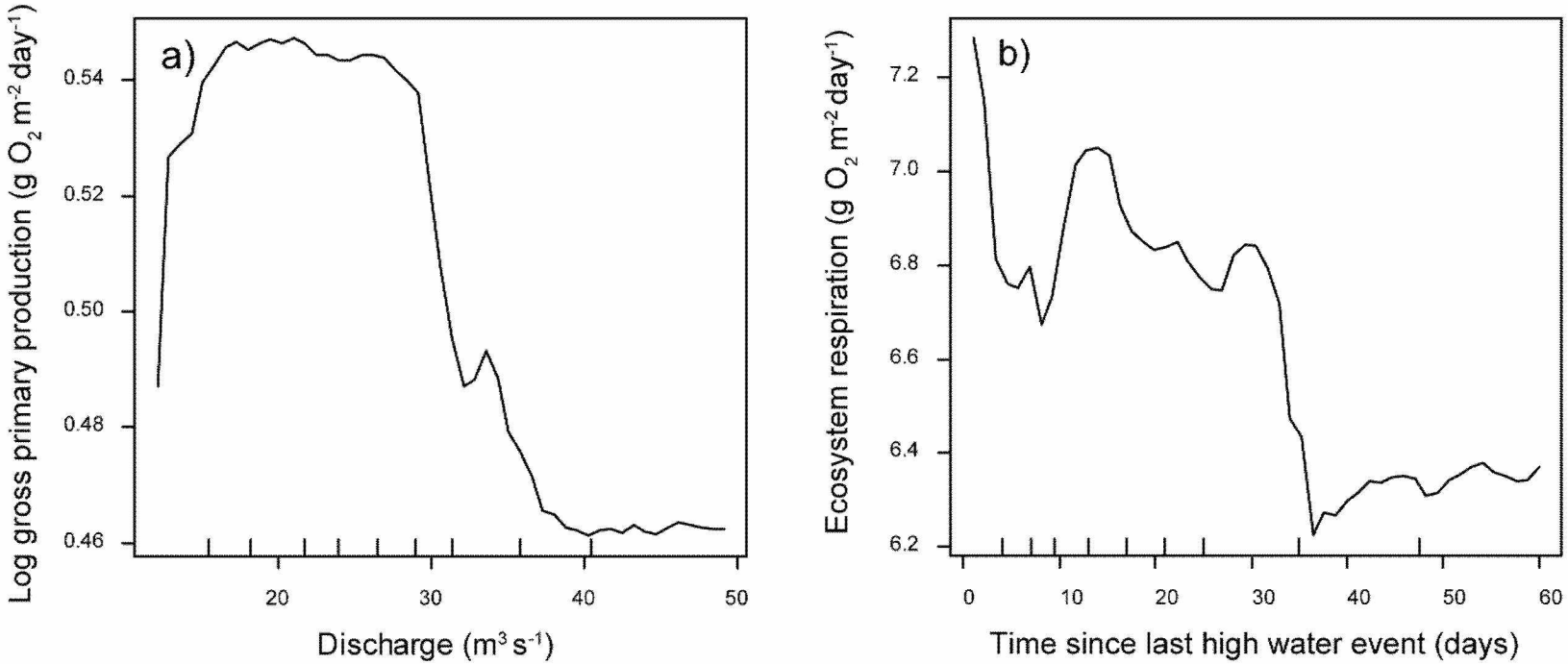

Fig. 6. (a) Effect of discharge on primary production rate, and (b) effect of time since last high water event on respiration rate in the Chena River, Alaska, USA, 2008-2009. These partial dependence plots show the influence of discharge or time since last high water event on the metabolism metric with the effects of all other variables removed. Inward-facing vertical dash marks on the x-axes represent deciles of data.

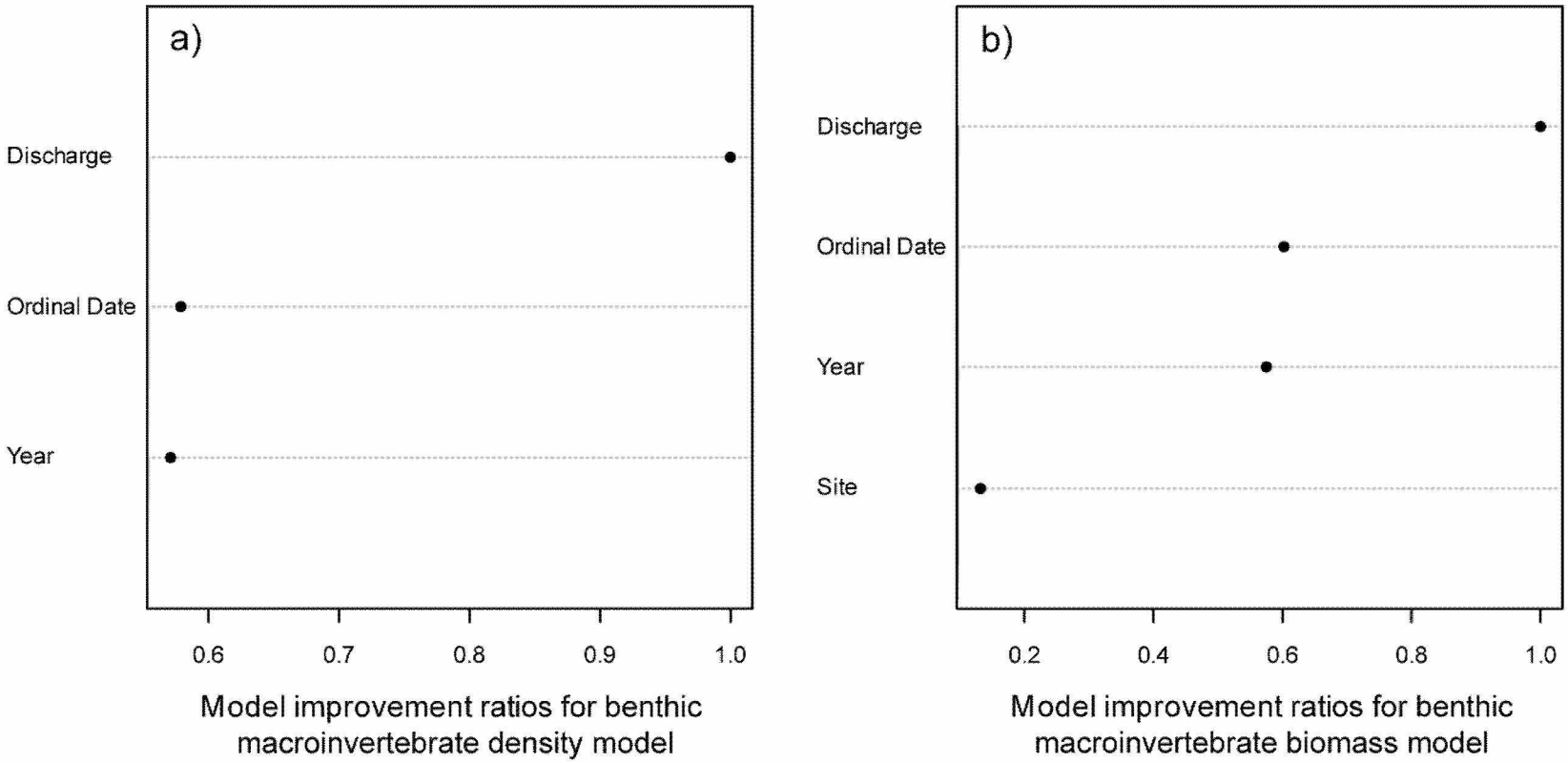

Fig. 7. Model improvement ratios and variable importance rankings for (a) benthic macroinvertebrate density and (b) benthic macroinvertebrate biomass Random Forests models in the Chena River, Alaska, USA, 2008-2009. The density model explains 58% of the variation in benthic macroinvertebrate densities in the Chena River, and the biomass model explains 39% of the variation in benthic macroinvertebrate biomass. If site and year are not included as predictor variables in the models, the density model explains the same amount of the variation in benthic macroinvertebrate densities (58%), and the biomass model explains 27% of the variation in benthic macroinvertebrate biomass.

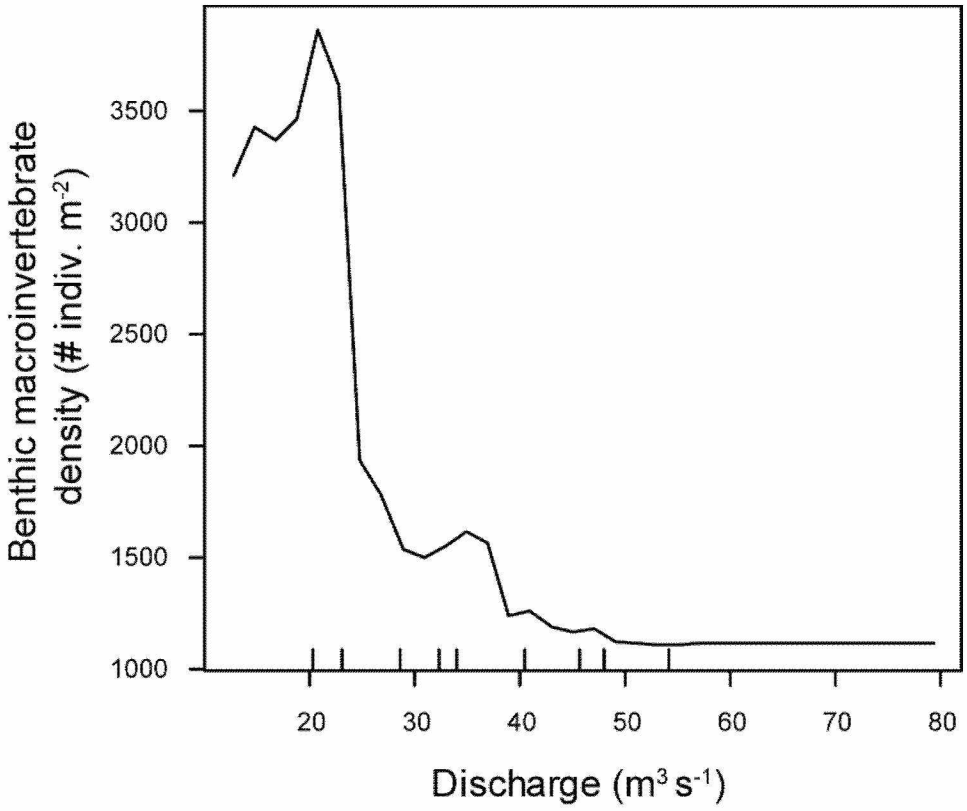

Fig. 8. Effect of discharge on benthic macroinvertebrate density in the Chena River, Alaska, USA, 2008-2009. This partial dependence plot shows the influence of discharge on benthic macroinvertebrate density with the effects of all other variables removed. Inward-facing vertical dash marks on the x-axis represent deciles of data.

Table 1 Mean (±SE) values and sample sizes for temperature, turbidity, photosynthetically active radiation, discharge, time since last high water event, soluble reactive phosphorous, nitrate-N + nitrite-N, ammonia-N, and dissolved organic carbon at four study sites along the Chena River, Alaska, USA, during 2008 and 2009. Exact site locations are noted on Figure 1. ND = no data. BD = below detection limit.

	2008				2009			
	Site 1	Site 2	Site 3	Site 4	Site 1	Site 2	Site 3	Site 4
Temperature (°C)	7.82 ± 0.25 *n* = 54	7.93 ± 0.32 *n* = 47	8.26 ± 0.40 *n* = 32	9.93 ± 0.42 *n* = 17	8.95 ± 0.24 *n* = 80	9.43 ± 0.19 *n* = 91	9.79 ± 0.18 *n* = 90	9.76 ± 0.19 *n* = 85
Turbidity (NTU)	37.9 ± 19.1 *n* = 54	40.7 ± 15.1 *n* = 47	140.5 ± 70.2 *n* = 32	204.3 ± 40.9 *n* = 17	120.7 ± 41.9 *n* = 80	107.5 ± 28.7 *n* = 91	10.4 ± 2.7 *n* = 90	74.4 ± 24.7 *n* = 85
Photosynthetically active radiation (mE s^{-1} m^{-2})	0.113 ± 0.010 *n* = 54	ND *n* = 47	0.174 ± 0.014 *n* = 32	0.225 ± 0.022 *n* = 17	ND *n* = 80	0.500 ± 0.034 *n* = 91	0.394 ± 0.026 *n* = 90	ND *n* = 85
Discharge (m^3 s^{-1})	50 ± 4 *n* = 54	56 ± 5 *n* = 47	58 ± 5 *n* = 32	59 ± 13 *n* = 17	34 ± 2 *n* = 80	33 ± 3 *n* = 91	36 ± 2 *n* = 90	36 ± 2 *n* = 85
Time since high water event (days)	8 ± 1 *n* = 54	9 ± 1 *n* = 47	13 ± 1 *n* = 32	22 ± 1 *n* = 17	23 ± 2 *n* = 80	24 ± 2 *n* = 91	25 ± 2 *n* = 90	25 ± 2 *n* = 85
Soluble reactive phosphorous (mg L^{-1})	BD *n* = 8	BD *n* = 8	0.002 ± 0.000 *n* = 8	0.002 ± 0.000 *n* = 8	BD *n* = 10	BD *n* = 10	0.002 ± 0.000 *n* = 10	0.002 ± 0.000 *n* = 10
Nitrate-N + nitrite-N (mg L^{-1})	0.286 ± 0.025 *n* = 8	0.245 ± 0.023 *n* = 8	0.226 ± 0.024 *n* = 8	0.223 ± 0.025 *n* = 8	0.233 ± 0.015 *n* = 10	0.209 ± 0.014 *n* = 10	0.189 ± 0.018 *n* = 10	0.187 ± 0.018 *n* = 10
Ammonia-N (mg L^{-1})	BD *n* = 8	BD *n* = 8	BD *n* = 8	BD *n* = 8	BD *n* = 10	BD *n* = 10	BD *n* = 10	BD *n* = 10
Dissolved organic carbon (mg L^{-1})	5.574 ± 1.036 *n* = 8	6.113 ± 1.171 *n* = 8	7.003 ± 1.155 *n* = 8	6.061 ± 1.200 *n* = 8	4.880 ± 0.730 *n* = 10	5.328 ± 0.684 *n* = 10	5.657 ± 0.859 *n* = 10	5.307 ± 0.894 *n* = 10

Table 2 Mean (±SE) values and sample sizes for gross primary production, ecosystem respiration, benthic macroinvertebrate density, and benthic macroinvertebrate biomass at four study sites along the Chena River, Alaska, USA, during 2008 and 2009. Exact site locations are noted on Figure 1.

	2008				2009			
	Site 1	Site 2	Site 3	Site 4	Site 1	Site 2	Site 3	Site 4
Gross primary production (g O_2 m^{-2} day^{-1})	3.91 ± 0.15 *n* = 54	2.16 ± 0.10 *n* = 47	1.64 ± 0.12 *n* = 32	1.97 ± 0.18 *n* = 17	2.59 ± 0.13 *n* = 80	1.92 ± 0.11 *n* = 91	2.06 ± 0.12 *n* = 90	1.87 ± 0.11 *n* = 85
Ecosystem respiration (g O_2 m^{-2} day^{-1})	8.93 ± 0.32 *n* = 54	5.05 ± 0.14 *n* = 47	5.10 ± 0.40 *n* = 32	4.20 ± 0.28 *n* = 17	8.95 ± 0.30 *n* = 80	6.48 ± 0.38 *n* = 91	7.15 ± 0.50 *n* = 90	6.56 ± 0.46 *n* = 85
Benthic macroinvertebrate density (# indiv. m^{-2})	2010 ± 984 *n* = 8	2108 ± 710 *n* = 8	2942 ± 1426 *n* = 7	1356 ± 551 *n* = 8	1116 ± 346 *n* = 10	1184 ± 266 *n* = 10	2267 ± 522 *n* = 9	1696 ± 420 *n* = 9
Benthic macroinvertebrate biomass (mg m^{-2})	330 ± 183 *n* = 8	411 ± 125 *n* = 8	542 ± 201 *n* = 7	160 ± 44 *n* = 8	245 ± 66 *n* = 10	242 ± 55 *n* = 10	395 ± 75 *n* = 9	222 ± 37 *n* = 9

Table 3 Macroinvertebrate taxa comprising five percent or more of the number of individuals found at four study sites along the Chena River, Alaska, USA, during 2008 and 2009. Exact site locations are noted on Figure 1. Percent of total number of individuals found at the given site and year indicated below taxon. Orders indicate individuals of that order, but unknown family.

2008				2009			
Site 1	Site 2	Site 3	Site 4	Site 1	Site 2	Site 3	Site 4
Simuliidae 45%	Chironomidae 60%	Chironomidae 51%	Chironomidae 45%	Simuliidae 31%	Chironomidae 42%	Chironomidae 52%	Chironomidae 53%
Chironomidae 19%	Ephemeroptera 7%	Ephemeroptera 19%	Ephemeroptera 14%	Chironomidae 22%	Simuliidae 15%	Ephemeroptera 11%	Simuliidae 13%
Heptageniidae 7%	Heptageniidae 7%	Simuliidae 7%	Nemouridae 7%	Heptageniidae 12%	Heptageniidae 11%	Simuliidae 9%	Ephemeroptera 9%
Ephemeroptera 6%	Hydracarina 5%		Simuliidae 7%	Ephemeroptera 8%	Ephemeroptera 7%	Heptageniidae 7%	Chloroperlidae 5%
Ephemerellidae 5%			Hydracarina 5%	Chloroperlidae 7%	Chloroperlidae 6%	Chloroperlidae 5%	
			Heptageniidae 5%	Oligochaeta 5%	Ephemerellidae 5%		
				Ephemerellidae 5%			

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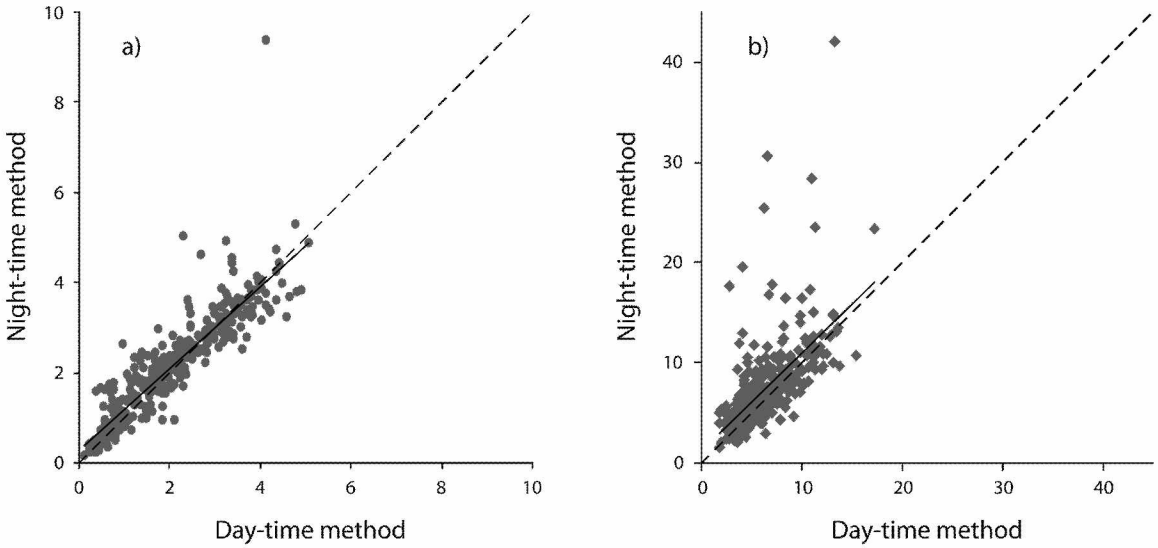
Appendix A

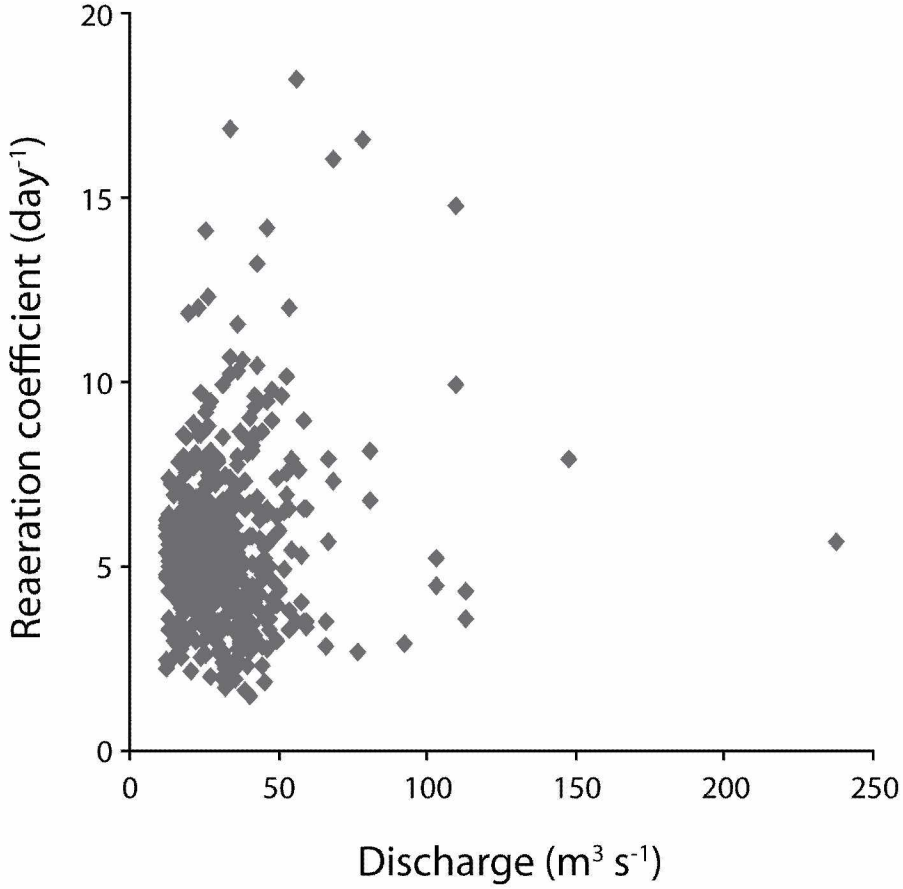
Comparison between night-time and day-time regression techniques for estimating river ecosystem metabolism rates



(a) Relationship between estimates of primary production rate, and (b) ecosystem respiration rate, made using the night-time and day-time regression techniques. Dashed lines indicate 1:1 relationship; solid lines represent linear regression lines. Metabolism estimates given by both methods were significantly correlated (Pearson correlations; primary production: $n = 370$, $r = 0.90$, $P < 0.001$; ecosystem respiration: $n = 370$, $r = 0.63$, $P < 0.001$).

Appendix B

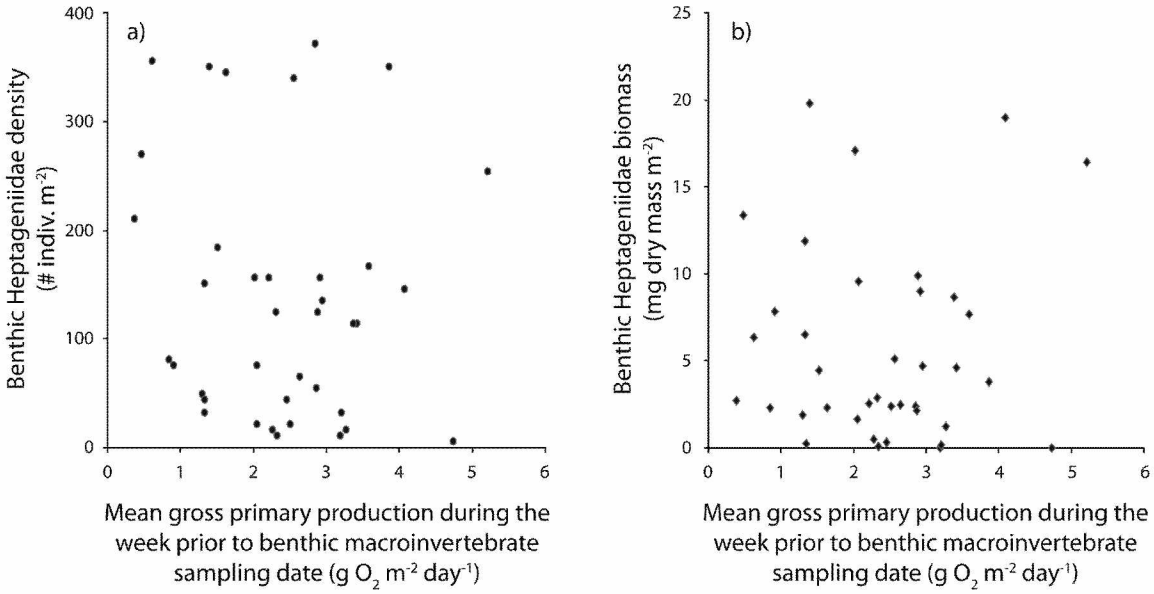
Correlation between reaeration coefficient and river discharge rate



Relationship between reaeration coefficient and river discharge rate. A two-sided Spearman correlation showed that reaeration coefficient value was not correlated with river discharge rate ($n = 539$, $P = 0.274$).

Appendix C

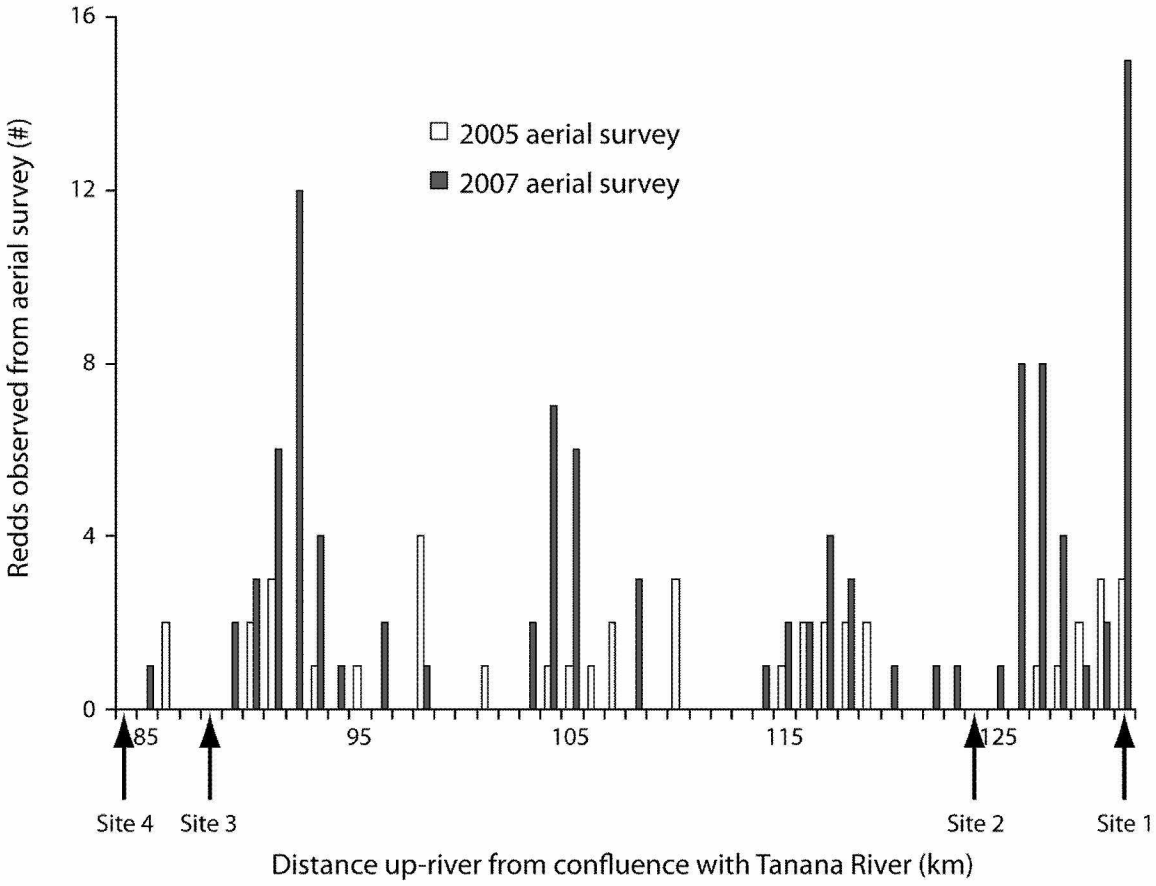
Correlation between benthic Heptageniidae density or biomass and rate of gross primary production during the week prior to benthic macroinvertebrate sampling



Relationships between (a) benthic Heptageniidae density, and (b) benthic Heptageniidae biomass, and rate of gross primary production during the week prior to benthic macroinvertebrate sampling. Two-sided Spearman correlations showed that gross primary production was not correlated with benthic Heptageniidae density ($n = 38$, $P = 0.401$) or benthic Heptageniidae biomass ($n = 38$, $P = 0.693$).

Appendix D

Distribution of salmon redds in relation to study sites



Distribution of salmon redds in the Chena River at and between the sites where the work described in this study was conducted, as determined by aerial survey in 2005 and 2007 (S. Decker, unpubl. data). Black arrows represent approximate location of study sites. During both 2005 and 2007, no redds were seen in the vicinity of Sites 2, 3, and 4; near Site 1, however, three redds were seen in 2005, and fifteen were spotted in 2007.

General Conclusions

The results of this study demonstrate the importance of considering environmental variables when assessing river ecosystem metabolism rates and benthic macroinvertebrate densities. We were able to explain 75% of the variance in primary production rates, and 52% of the variance in ecosystem respiration rates in the Chena River during the summers of 2008 and 2009. Much of this variance (63% of the total variance in primary production rates, and 31% of the total variance in ecosystem respiration rates) was attributed to the environmental variables we studied, particularly river discharge rates and length of time between high water events. Primary production rates peaked at intermediate discharge rates; intermediate river flows apparently represent a balance between the positive affects of nutrient inputs on primary production rates (Stevenson, 1990) and the negative affects of decreased light availability and increased water velocity (Izagirre *et al.*, 2008; Young, Matthaei & Townsend, 2008). Respiration rates were highest directly following a high water event and declined over time after that. This short-term spike in respiration rates could have been due to increased availability of organic matter, as has been suggested for headwater streams where the same stimulation in respiration rates after storms has been observed (Roberts, Mulholland & Hill, 2007).

Though our results showed the importance of discharge and flow regime for predicting metabolism rates, they also highlighted the importance of some environmental factor or factors that differed between the study sites we were not able to identify. During both 2008 and 2009, metabolism rates were substantially higher at the furthest up-river site than at the other three study sites. One possible explanation for the difference in metabolism rates among the study sites is that there may have been more nutrients and organic matter available at the upper-most study site due to differences in spawning salmon density among the sites. Though we were unable to conclusively determine what was responsible for this difference in metabolism rates among the study sites, that it occurred shows that there can be environmental differences on a small spatial scale that have a large impact on metabolism rates. The farthest up-river site was separated by the

next study site by about 7.5 river km, and that distance was enough to separate the sites in a functional, as well as spatial, sense. Research conducted in a grassland river suggests that there may be longitudinal patterns in river ecosystem metabolism rates (Young & Huryn, 1996); however, the pattern in ecosystem metabolism rates in the Chena does not appear to be simply a longitudinal one, at least on a river-wide spatial scale, as there were differences between the upper-most site in our study and the other three sites, but no clear longitudinal pattern.

We did not uncover large differences in benthic macroinvertebrate density and biomass between the four study sites, and study site was not identified as an important predictor of benthic macroinvertebrate density or biomass, suggesting that the differences in metabolism rates between our study sites that we found were not due to differences in benthic macroinvertebrate density; though differences in benthic macroinvertebrate community composition between the study sites may be one explanation for the differences in metabolism rates between the sites. Surprisingly, primary production rates were also not identified as an important predictor of benthic macroinvertebrate density or biomass. Though algal activity is a major driver of primary production rates in rivers (Young *et al.*, 2008), and algae is an important food source for aquatic macroinvertebrates (McCutchan & Lewis, 2002), research has not shown a relationship between primary production rates and macroinvertebrate densities (Hawkins & Sedell, 1981). Our results support those of Hawkins and Sedell (1981); our models did not identify primary production rates as important for predicting benthic macroinvertebrate density or biomass. This could be due to the lack of periods characterized by high and sustained rates of primary production during our study. We found that river discharge rate was particularly important for predicting benthic macroinvertebrate densities and biomass, and both macroinvertebrate metrics displayed a negative relationship with river discharge. This finding is consistent with previous research identifying several different discharge metrics as associated with limits on macroinvertebrate assemblages (Konrad, Brasher & May, 2008).

This study demonstrates the importance of the influence of environmental variables on the basal food web resources that sustain organisms at higher trophic levels, including fish. River discharge rate and flow regime were especially important for predicting river ecosystem metabolism rates, as well as benthic macroinvertebrate densities and biomass in this study. Furthermore, our results suggest that phosphorus may have been limiting primary production in the Chena River, a conclusion that previous research on the Chena River has also shown (Cai *et al.*, 2008). Our findings are important because they represent a snap-shot of the baseline conditions in the Chena River; in order for metabolism rates to be a useful indicator of river health, it is necessary to first understand how natural variation influences them (Clapcott *et al.*, in press). Thus, our study represents an important step towards being able to use metabolism rates as indicators of river health in interior Alaska. Our results also suggest ways in which basal food web resources could be affected by human-caused changes to the river system, for example, dam building and increased nutrient loading. The effects of these changes can cascade throughout a river food web because of the impact they have on basal food web resources, particularly metabolism rates and benthic macroinvertebrates (Slavik *et al.*, 2004). Therefore, river resource managers should consider the potential effects on metabolism rates and benthic macroinvertebrates before implementing management plans that will influence river discharge rates, flow regime, and nutrient loading.

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